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Response of C_3 and C_4 Plant Systems Exposed to Heavy Metals for Phytoextraction at Elevated Atmospheric CO_2 and at Elevated Temperature

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1. Introduction

Increasing concentration of CO_2 in the lower atmosphere and an increase in average annual temperature are two major factors associated with global climate change. Researches show profound impact of climate change on the global primary productivity (Krupa, 1996; Kimball, 1983). Apart from the climate change, environmental contamination especially of those chemicals are non degradable and persist in the environment for long e.g., chlorinated pesticides, and heavy metals. In fact, heavy metal ions such as Cu^{2+}, Zn^{2+}, Mn^{2+}, Ni^{2+}, Fe^{2+}, and Co^{2+} are essential in trace amounts for growth of organisms (Kunze et al., 2001; Choudhry et al., 2006), however; the excessive amounts of these metal ions along with other non essential metals such as Pb^{2+}, Cd^{2+}, and Hg^{2+} aggravated the menace to an alarming stage (Kamal et al., 2004). Our knowledge regarding the non degradable contaminants has enhanced in last two decades however; more researches are needed for the mitigation and to reduce the introduction of any new contaminant in to the environment. Researchers all over the world endeavoured to resolve the problem and have developed several techniques to restore the quality of environment. The only solution to the problem associated with non degradable contaminants is the removal from the contaminated sites (Lasat, 2002).

Phyto-remediation has achieved a top priority among the activists and scientists because of its cost effectivity and sustainable nature. Voluminous literature based on extraneous researches is available today supporting the use of plant systems for the removal of heavy metals from the contaminated area (Khan et al., 1998; Ebbs & Kochian, 1998; Hinchman et al., 1998; Srivastava & Purnima, 1998; Pulford & Watson, 2003; Wilde et al., 2005) and the references quoted there in. Since plants respond differently in altered environmental conditions viz., nutrient status of soil, water availability, pollution, elevated CO_2 and elevated temperature and humidity, it is imperative to review the performances and responses of plant systems especially when growing in contaminated sites with heavy metals at extreme environmental conditions like that are posed by the global climate change. However; prior to review the responses of C_3 and C_4 plant systems lets consider the general aspects regarding heavy metals, contamination, toxicity and phytoremediation.

1.1 Heavy metals (HMs): Contamination and toxicity

Heavy metals (HMs) form the main group of inorganic contaminants (Alloway, 1990). There are number of instances worldwide polluted with HMs naturally as well as anthropogenically. Industries especially metallurgical, foundries, mining, tanneries and thermal power plants have significant importance as these generate huge amounts of waste containing higher concentrations of toxic metals (Gupta et al., 2010; Aguilera et al., 2010). HMs are defined as the transition elements having density more than 5 gm cm^{-3}, and recently have been defined as the Class – B (border line) (Nieboer & Richardson, 1990). Out of 90 naturally occurring elements, 53 are heavy metals (Weast, 1984) out of which only few (around 17) metals are biologically significant because these are readily available to living cells (Weast, 1984; Pickering, 1995). Action of HMs leading toxicity in living cells depending upon several physico-chemical factors such as redox potential (of surrounding medium and inside the cells). Because of being transitional elements, several ions of different valence states are quite common of same metal for e.g., four species of chromium (Cr) viz., Cr, Cr^{3+}, Cr^{4+}, and Cr^{6+}. Most of the HMs usually form cations e.g., Cu^{2+}, Zn^{2+}, Mn^{2+}, Ni^{2+}, Fe^{2+}, and Co^{2+} (table 1). There exist two groups of HMs viz., redox active and redox inactive (Schützendübel & Polle, 2002). Once toxic metals are present in the environment they eventually become a part of abiotic and biotic components of an ecosystem (Galloway et al., 1982), posing toxicity to the living organisms interacting with each other. Metals with low redox potential (Eh value) has very little significance for biological redox reactions. Auto-oxidation and Fenton type reactions are supposed to be the cause of free radicals generation especially the reactive oxygen species (ROS) from HMs causing injury the cells and cell organelles (Jones et al., 1991; Shi et al., 1993; Stohs & Bagchi, 1995). Heavy metals are especially toxic because of their ability to bind with proteins and prevent DNA replication as these can bind strongly to oxygen, nitrogen and sulphur atoms (Nieboer & Richardson, 1980) and inactivate enzymes by binding to cysteine residues (Schützendübel & Polle, 2002).

Common occurring metals	Toxic ionic species
Cd (Cadmium)	Cd^{2+}
Co (Cobalt)	Co^{2+}
Cu (Copper)	Cu^{2+}, Cu^{3+}
Cr (Chromium)	Cr^{6+}
Fe (Iron)	Fe^{3+}
Hg (Mercury)	Hg^{2+}, Hg^{3+}
Mn (Manganese)	Mn^{2+}, Mn^{3+}
Ni (Nickel)	Ni^{2+}, Ni^{3+}
Pb (Lead)	Pb^{2+}
Zn (Zinc)	Zn^{2+}

Table 1. Heavy metals of common occurrence and their toxic ionic species

1.2 Phyto-remediation of HMs: General aspects

Removal of any non-degradable, undesirable, inorganic or organic contaminant or pollutant with the help of plants is commonly termed as phytoextraction and the process is called phyto-remediation. Phyto-remediation is a cost effective and a sustainable way to mitigate the environmental pollution that has attracted scientists and policy makers all over the world. The only remedy for heavy metal contamination is to remove and reuse (Chojnacka, 2010). Phytoextraction, rhizo-filtration and phytostabilization are the technical processes occur in a plant simultaneously to make up *in-situ* phyto-remediation (Suresh & Ravishankar, 2004). Phyto-remediation technique has technical advancement over the traditional chemical and physical techniques to remove contaminants from the environment (Garbisu & Alkorta, 2001). Phyto-mining which signifies the recovery of rare and valuable trace metal contaminants from the harvested biomass (net primary product) offers a great significance in metal removal. Metal contamination is removed by plants capable of defending the toxic manifestations by three distinct ways viz., (1) restrict entry of metals in to the soft growing tissues by excluding metals from the metabolic pathways, (2) restrict entry to the shoot as the metals is accumulated by the roots, (3) accumulation of metals in different parts (Kamal et al., 2004). Successful restoration is however; dependent on the selection of plant species based on the method of their establishment along with the knowledge of growth regulating factors (Tu & Ma, 2003). Ideally plants, growing fast, capable of producing higher biomass, and able to tolerate and accumulate high concentrations of HMs in shoots are best suited for phyto-remediation. *Brassicaceae* family of C_3 plants have metal accumulating capability to greater extent (Kumar et al., 1995). Phyto-remediation is most useful when contaminants are within the root zone of the plants i.e., top soil (up to 1 meters) (Wilde et al., 2005). Biochemically plants are equipped to protect their selves from the toxicity of metals as they synthesize Cys-rich (Cysteine rich), metal – binding peptides including phyto-chelatins and metallothioneins (-SH group containing peptides) (Jonak et al., 2004) to relocate HMs by chelation and sequestration in the vacuole (Clemens, 2001) on the other hand, membrane transport systems provide plants tolerance for toxic metals (Hall & Williams, 2003).

2. C_3 and C_4 plant system: An introduction

In nature three different plant systems exist viz., C_3, C_4 and CAM, characterized on the basis of CO_2 trapping mechanisms, however; C_4 and CAM plants essentially follow C_3 pathway to trap CO_2 as an initial step. C_4 is a characteristic photosynthesis syndrome of angiosperms. In general *phosphoenolpyruvate carboxylase* (EC 4.1.1.31, PEPC) enzyme is widespread among all plants, including C_3 (e.g., *Pisum sativum, Gossipium hirsutum, Oryza sativa, Brassica campestris, Triticum aestivum, Avena sativa*) C_4 (e.g., *Zea mays, Saccharum officinarum, Sorghum spp., Vetiveria zizanioides, Cyanadon dactylon*) and CAM (e.g., members of Orchidaceae, Polypodiaceae (ferns)) species and is responsible for the initial carbon fixation in C_4 and CAM plants (O' Leary, 1982). CAM plants are very few in nature and have very little significance for this review purpose. C_3 and C_4 plants have unique carbon trapping mechanisms. The general enzymatic system involves in CO_2 fixation in C_3 and C_4 are Ribulose-1-5-bisphosphate carboxylase oxygenase (Rubisco EC 4.1.1.39) and phosphoenolpyruvate carboxylase (PEPC), NADP-malic enzyme (NADP-ME), Pyruvate, phosphate dikinase (PPDK) respectively. The leaves of C_4 plants display Kranz anatomy whereby an outer layer of mesophyll cells containing chloroplast surrounds vascular bundles with an inner layer of bundle sheath cells (Dengler & Nelson, 1999). In C_3 plants mesophyll cells are devoid of chloroplast and CO_2 is fixed in bundle sheath cells by Rubisco. Chloroplasts of C_3 plant contain a complete Calvin cycle and are able to assimilate CO_2 to convert it to the principle 3 carbon compound (triose phosphate), on the other hand CO_2 is distributed in two cells viz., mesophyll and bundle sheath in C_4 plants and converted primarily in 4 carbon compound (acid oxaloacetate) by the action of PEP-C in mesophyll cells (Ueno, 2001) which is then transported in bundle sheath cells where by the acids from mesophyll cells provide carbon dioxide. Extensive research literature is available on the comparative account of C_3 and C_4 plant systems (Du & Fang, 1982; Rajendrudu & Das, 1982; Matsuoko & Hata, 1987; Wand et al., 1999; Ueno, 2001; Winslow et al., 2003; Derner et al., 2003; Sage, 2004; Edwards et al., 2005; Niu et al., 2006; Caird et al., 2007; Bräutigam et al., 2008; Tang et al., 2009; Weber & Caemmerer, 2010, Doubnerová, & Ryšlavǎ, 2011) however; very few and scattered information is available on the comparative account of C_3 and C_4 plants and their growth performances under extreme environmental conditions. In this chapter, collective information based on the established researched facts from all over the world regarding the responses of C_3 and C_4 plants growing under stressful environment have been reviewed.

C_4 plants have higher rates of photosynthesis than C_3 plants (Sage, 2004; Weber & Caemmerer, 2010). Photosynthesis in C_4 plants does not saturate but increases at high light intensities and can continue at very low CO_2 concentrations (Sage, 2004; Bräutigam et al., 2008). Subsequently, these plants have rapid growth rates and higher biomass and economic yields as compared to the C_3 plants. There are evidences from researches that C_4 plant such as vetiver grass (*Vetiveria zizanioides* L. Nash) can withstand harsh environmental conditions (Truong & Baker, 1998, Chen et al., 2004, Chiu et al., 2006; Srivastava et al., 2008). A comparative study performed on two separate species belonging to C_3 and C_4 systems respectively show that the environmental tolerance depends on the high biomass production which is higher in case of C_4 plants (Ye et al., 1997; Ali et al., 2002). However; there is lack of information regarding the biochemical differences among C_3 and C_4 plant systems exposed to toxic environment for e.g., the extent of detoxification mechanism, mycorrhization, proteomes (expression of genes). The researches carried out for the investigations of toxic response of particular plant variety belonging to C_3 and C_4 type indicate that there is a high tolerance in C_4 plants as compared to the C_3 plants which may or may not be true for the entire group of plants belonging to these systems (Chapin, 1991; Ali et al., 2002; Niu et al., 2006). C_4 photosynthesis allows fast biomass accumulation with high nitrogen and water use efficiency (Leegood & Edwards, 1996; Sage, 2004) which is desired set of traits to increase the productivity of crop plants (Matsuoka et al., 1998) and a required character for successful phytoremediation.

3. Plant's response, environmental contamination and environmental factors

Prior to study the response of plant systems for any particular measurable environmental factor such as heavy metal concentration in water or soil, or set such as soil related factors including physical as well as chemical, it is required to take measurable responsive quantity such as biomass, growth rate, and enzyme kinetics. Small changes in environmental conditions may cause significant alterations in growth rates therefore growth rate is preferred as the primary and essential parameters to monitor impact of any environmental factor. In general plants achieve variety of mechanisms providing tolerance or resistance against environmental heights. The locally adapted plants (Eco-types) are well versed with such mechanisms making the species capable to survive in their corresponding environmental conditions. The response of plants (C_3 and C_4 plant systems) exposed to any undefined environmental extremity should not be considered alone because the response of a plant against any (favorable or stressful) conditions is a result of collective influence of stress and prevailed environmental conditions for e.g., in warmer conditions C_3 plants do not respond positively however; C_4 does and vice versa which is evident from the studies of C_3 and C_4 intermediate plant species such as *Phragmites australis* (Zheng et al., 2000) and *Eleocharis vivipara* (Ueno, 2001). Continuous altering weather conditions, soil related factors, light intensity, water availability, nutrient status, temperature, humidity, and evaporation coefficient make the *in-situ* experimentation very difficult and the response measurement of plants becomes dubious and assignment of the reason for a particular response becomes tedious affair. There are many other factors that may or may not be responsible for a particular response, for e.g., plants growing in mine tailings may exhibit negative growth impacts, a response which is usually attributed to the presence of toxic metals however; the influence of prevailed environmental conditions remain silent which must be addressed. In general environmental stress conditions alter the plant metabolism e.g., photosynthesis.

4. Affect of climate change on C_3 and C_4 plant systems

Studies show that elevated CO_2 often enhances biomass more in C_3 (41 – 44%) than in C_4 plants (22 – 33%) (Poorter, 1993; Wand et al., 1999) however; more advanced studies suggest that certain environmental factors such as water and nutrient availability can modify plant response to CO_2 enrichment (Oren et al., 2001; Derner et al., 2003; Hikosaka et al., 2005). Although increased biomass in response to elevated CO_2 are often greater in C_3 plants, C_4 plants are often more resistant to high temperature and better adapt to low nutrient environments (Edwards et al., 2005). This suggests that even with elevated CO_2 levels, C_4 plants are able to maintain their competitive advantage over C_3 plants under environmental extremities (table 2). No any direct evidence is available on the responses of C_3 and C_4 plants used for environmental mitigation purposes at elevated CO_2 and temperature. However; the researches carried out for the investigations of toxic response of plants belonging to C_3 and C_4 system indicate high tolerance in C_4 plants as compared to the C_3 plants that can not be stipulated as a generalization for the entire group of plants belonging to these systems (Leegood and Edwards, 1996). C_4 photosynthesis allows fast biomass accumulation with high nitrogen and water use efficiency (Leegood and Edwards, 1996; Sage, 2004) and is a desired trait to increase the productivity of crop plants (Matsuoka et al., 1998). Studies of Ehleringer & Björkman (1977) showed that C_3 plants were favored at low temperature while the high temperature favored C_4 plants. The response of C_3 and C_4 plants and their global distribution has been proved to be a function of temperature (Lloyd & Farquhar, 1994). However; extensive research reports are available on the temperature and distribution of the C_3 and C_4 plants (Dickinson & Dodd, 1976; Ehleringer et al., 1997; Sage et al., 1999; Winslow et al., 2003).

In general C_3 plants are favored by low temperature thus distributed more at higher altitudes and C_4 plants are favored by high temperature. Riesterer et al. (2000) suggested that essentiality of water availability for both (C_3 and C_4) plant systems to grow under seasonal temperature variations. In C_4 plant system photo-respiration is rarely greater than 5% of the rate of photosynthesis; in C_3 plants, it can exceed 30% of the rate of photosynthesis above 30^{0}C (Sage & Pearcy, 2000). Because of such improvements, C_4 plants have higher productive potential, and greater light, water and nitrogen use efficiency of both photosynthesis and growth (Evans, 1993; Brown, 1999).

Response Parameters	**C_3 under elevated CO_2 & temperature**	**C_4 under elevated CO_2 & temperature**	**References**
Photosynthetic activity	Cold conditions preferred	Higher temperature resistant	Weber & Caemmerer, 2010; Ueno, 2001
Photorespiration	Can exceed 30%	Hardly achieve 5%	Sage, 2004
Light use efficiency	Lesser	Greater	Bräutigam et al., 2008; Evans, 1993
Biomass (gm dry wt.)	Slightly < C_4 (33%)	Slightly > C_3 (44%)	Sage, 2004; Wand et al., 1999
Mycorrhization	Lesser	Higher	Tang et al., 2009; Treseder, 2004
Water use efficiency	Less efficient	Highly efficient	Derner et al., 2003; Winslow et al., 2003
Nitrogen Use efficiency	Less efficient	Highly efficient	Niu et al., 2006; Edwards et al., 2005
Stomatal conductance	High	Lower	Caird et al., 2007

Table 2. Performance of C_3 and C_4 plants under elevated carbon dioxide (CO_2) and at elevated temperature

5. Climate change and microbial association in C_3 and C_4 plant systems

Arbuscular mycorrhizal (AM) association with roots of plants and is one of the well accepted factors responsible for their growth on disturbed sites such as heavy metal contaminated soils (Khade & Adholeya, 2009). In addition, microbial associations often provide some sort of immunity (Srivastava et al., 2008) to plants against the environmental extremities (Gaur & Adholeya, 2004). A unique feature added to plants is that, elevated CO_2 often increases in mycorrhizal colonization in the roots (Rilling et al., 1998; Treseder, 2004) because elevated CO_2 enhances carbon allocation to roots (Rilling & Allen, 1998). Studies also showed increase in mycorrhizal infection rate with elevated CO_2 levels (Staddon & Fitler, 1998; Treseder, 2004; Hu et al., 2005). Monz et al. (1994) reported that the enhancement of mycorrhizal colonization by elevated CO_2 was higher in C_4 plants than in C_3 plants. This CO_2 enhanced mycorrhizal colonization may alter plant nutrient uptake and plant interactions with their neighbors (O'Conner et al., 2002; Chen et al., 2007) particularly if mycorrhizae in the coexisting species respond differently to CO_2. Interestingly, C_4 plants are more dependent on mycorrhizae for growth and productivity than C_3 plants (Wilson & Hartnett, 1998). Altered responses have been reported in C_3 and C_4 plants because of mycorrhizae under low nutrient environment (Tang et al., 2006). In agricultural systems most troublesome weeds especially those are difficult to control belong to C_4 plant systems, while most of the major crops are C_3 plants (Patterson, 1995; Fubrer, 2003). Tang et al. (2009) reported the CO_2 enhanced arbuscular mycorrhiza (AM) affect competition for light between C_4 and C_3 plants resulting in that shoot biomass of C_4 plants was higher than in C_3 under elevated CO_2.

6. Biochemical response evaluation of C_3 and C_4 plant systems exposed to heavy metal stress under elevated CO_2 and temperature

In general, the growth of plants increase under elevated atmospheric CO_2 (Poorter et al., 1996), depending upon the prevailing trends of certain anionic nutrients such as PO_4^{-3}, and NO_3^{-1}. Voluminous literature in this regard indicates that plants growing well even under stressful conditions if provided with nutrients. Since C_4 plants have biochemical advantages over C_3 plant systems (table 3) as C_4 photosynthesis is characterized by excessive CO_2 at the site of Rubisco, that helps reducing the rate of photorespiration and increasing net carbon

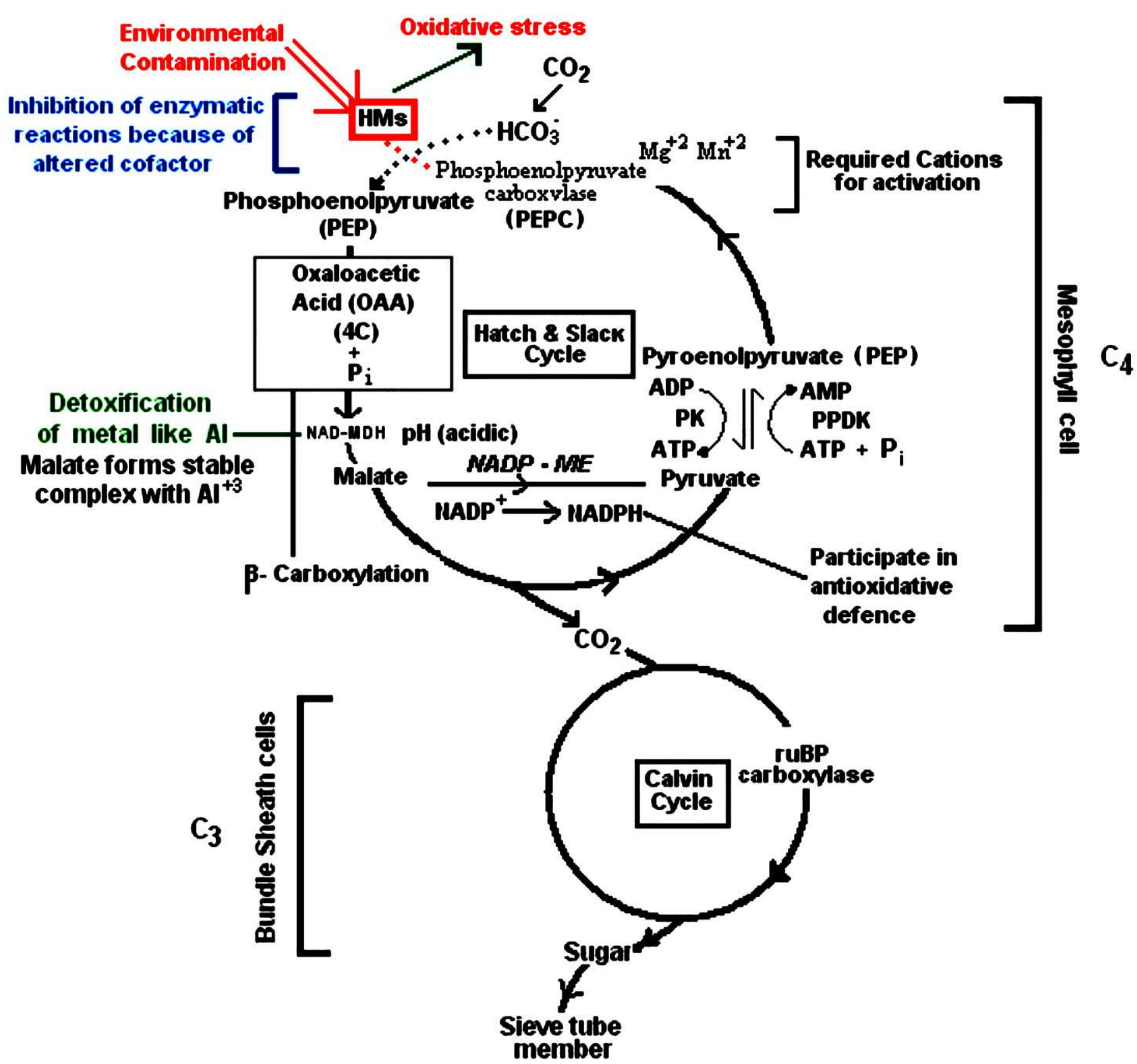

Fig. 1. Photosynthesis diagram of C_3 and C_4 plant showing the role of PEPC enzyme in heavy metal response whereas Phosphoenolpyruvate carboxylase (PEPC) enzyme acts as metal detoxifying agent.

dioxide assimilation, in other words the biomass. The plants viz., C_3 and C_4 exposed to HMs stress under elevated atmospheric CO_2 and at elevated temperature follow the same trend as in normal conditions however; there are significant alterations in biochemistry of photosynthesis of both types of plant systems. Figure 1 shows the effect of HMs on the enzymes those catalyses the photosynthetic reactions e.g., PEPC, PPDK (pyruvate phosphoenol dikinase), NADP-ME (NADP dependent malic enzyme) (Doubnerová, & Ryšlavă, 2011). PEPC enzyme that catalyze the reaction of bicarbonate and phosphoenol pyruvate (PEP) to yield 4 C acid compound oxaloacetic acid (OAA) need divalent metal ions such as Mg^{+2} and Mn^{+2} for activation. These metal ions along with other such as Fe and Zn are cofactors and may be replaced by the HMs that inhibit the activity of enzyme resulting into less CO_2 supply at the rubisco site thereby reducing the net productivity.

Elevated atmospheric CO_2 can disrupt the pH (alkalization) of cell sap by forming HCO_3^{-1}, which induces the activity of PEPC. Despite having toxic manifestations of HMs, the abundant PEPC favors the production of OAA in C_4 plants, which is further converted into acidic malate by the action of NAD dependent malate dehydrogenase enzyme (NAD-MDH EC 1.1.1.37). This NAD-MDH enzyme also act as detoxifying agent as it also catalyze the formation of stable compounds of malate and metals such as aluminum (Ma & Furukawa, 2003). C_3 plants however; are devoid of such defense mechanisms as PEPC is not the primary carbon dioxide fixing enzymes and face the oxidative stress caused by HMs. Since photosynthetic efficiency depends largely on the activity of rubisco (Sage, 2004), elevated atmospheric CO_2 increases the photorespiration in C_3 plants as a result of oxygenase activity of rubisco increasing the oxidative conversion of metals present in the cell. The oxidative conversion of metals in C_3 plant is also favored by the higher atmospheric temperature (Du & Fang, 1982). The oxidation of metals in living organisms is thiol (-SH) containing compound mediated with the hydrogen peroxide (H_2O_2) catalase complex. Catalase is present in peroxisomes of plant cells. In C_3 plants high photorespiration rates as a result of elevated concentration of CO_2, peroxisomes are large and numerous while in the C_4 plants the peroxisomes of mesophyll cells are small and fewer in number (Tolbert, 1971). The *milieu interior* of cells of C_4 plants is highly reductive thus prevent the oxidative conversion of metals.

7. Conclusion

Global climate change coupled with the environmental contamination with non-degradable substances such as pesticides, organic compounds and heavy metals are the well known fact of today's world. Among these the heavy metal contamination is inevitable in the modern age because of rapid urbanization. The health hazards of this non-degradable environmental contaminant are alarming as evident from the researches all over the world. The only solution is to extract or remove metal ions from the contaminated media. Phytoextraction is the most cost effective and environmentally sound technology for the removal of heavy metals whereby plants are employed to remove safely the toxic metal ions. C_3 and C_4 both are well researched for their ability to survive the environmental extremities such as that of climate change. Heavy metals are taken up by both types of plants however; we conclude with the findings that C_4 are the most appropriate plant system for phytoextraction although there are few benefits associated with C_3 such as higher biomass under elevated atmospheric carbon dioxide, which is required characteristic for removal of environmental contaminants. In addition to this microbial association is also favored at elevated CO_2 that provide tolerance to the plants therefore only biomass can not be ascertained as the measure responsible for the survival of C_3 or C_4 plants in conditions like global climate change.

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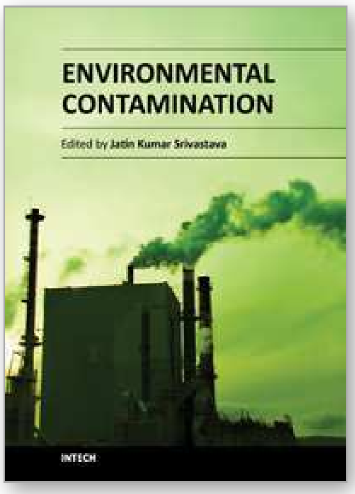

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Nature minimizes the hazards, while man maximizes them. This is not an assumption, but a basic idea of the findings of scientists from all over the world. The last two centuries have witnessed the indiscriminate development and overexploitation of natural resources by man causing alterations and impairment of our own environment. Environmental contamination is the result of the irrational use of resources at the wrong place and at the wrong time. Environmental contamination has changed the lifestyle of people virtually all over the world, and has reduced the extent of life on earth. Today, we are bound to compromises with such environmental conditions, which was not anticipated for the sustenance of humanity and other life forms. Let us find out the problem and its management within this book.